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Abstract: Sexual size dimorphism (SSD) varies widely across and within species. The differential equilibrium model of SSD explains di- morphism as the evolutionary outcome of consistent differences in natural and sexual selection between the sexes. Here, we comprehensively examine a unique cross-continental reversal in SSD in the dung fly, Sepsis punctum. Using common garden labo- ratory experiments, we establish that SSD is male-biased in Europe and female-biased in North America. When estimating sexual (pairing success) and fecundity selection (clutch size of female partner) on males under three operational sex ratios (OSRs), we find that the intensity of sexual selection is significantly stronger in European versus North American populations, increasing with male body size and OSR in the former only. Fecundity selection on female body size also increases strongly with egg number and weakly with egg volume, however, equally on both continents. Finally, viability selection on body size in terms of intrinsic (physiological) adult life span in the laboratory is overall nil and does not vary significantly across all seven populations. Although it is impossible to prove causality, our results confirm the differential equilibrium model of SSD in that differences in sexual selection intensity account for the reversal in SSD in European versus North American populations, presumably mediating the ongoing speciation process in S. punctum.

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Sexual selection accounts for the geographic reversal of sexual size dimorphism in the dung fly, *Sepsis punctum* (Diptera: Sepsidae)

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ABSTRACT

Sexual size dimorphism (SSD) varies widely across and within species. The differential equilibrium model of SSD explains dimorphism as the evolutionary outcome of consistent differences in natural and sexual selection between the sexes. Here we comprehensively examine a unique cross-continental reversal in SSD in the dung fly, *Sepsis punctum*. Using common garden laboratory experiments, we establish that SSD is male-biased in Europe and female-biased in North America. When estimating sexual (pairing success) and fecundity selection (clutch size of female partner) on males under three operational sex ratios (OSR), we find that the intensity of sexual selection is significantly stronger in European vs. North American populations, increasing with male body size and OSR in the former only. Fecundity selection on female body size also increases strongly with egg number and weakly with egg volume, however equally on both continents. Finally, viability selection on body size in terms of intrinsic (physiological) adult lifespan in the laboratory is overall nil and does not vary significantly across all seven populations. Although it is impossible to prove causality, our results confirm the differential equilibrium model of SSD in that differences in sexual selection intensity account for the reversal in SSD in European vs. North American populations, presumably mediating the ongoing speciation process in *Sepsis punctum*.

KEYWORDS

Sepsid flies; body size; natural selection; sexual selection; population differentiation; speciation

INTRODUCTION

Evolutionary biologists largely agree that divergence in sexual dimorphism and mating behavior is frequently driven by sexual selection (Andersson 1994; Arnqvist et al. 2000; Gray and Cade 2000; Panhuis et al. 2001; Boake 2005; Gavrilets and Hayashi 2005; Ritchie 2007). Differences in body size between the sexes, or sexual size dimorphism (SSD), is ubiquitous but variable across the animal kingdom. Species and even populations within a species can differ greatly in the direction and extent of SSD, and there are numerous studies exploring the evolutionary mechanisms underlying this variation (Andersen 1994; Fairbairn 1997; Blanckenhorn 2000; Ding and Blanckenhorn 2002; Drovetski et al. 2006; Blanckenhorn et al. 2007a; Fairbairn et al. 2007; Serrano-Meneses et al. 2007; Stillwell and Fox 2007; Teuschl et al. 2007). It is established that body size affects reproductive success via different mechanisms in the sexes, so the optimal size associated with the maximum fitness often varies for males and females. According to the differential equilibrium model of the evolution of SSD, dimorphism in body size arises when the net effects of sexual and natural selection differ between the sexes (Price 1984; Andersson 1994; Preziosi and Fairbairn 2000; Blanckenhorn 2000). For instance, most mammals and many birds exhibit male-biased SSD, which is primarily attributed to greater mating success of larger males due to male-male competition (via access to territories and/or females) or female choice (Abouheif and Fairbairn 1997; Moore and Wilson 2002). SSD is typically reversed among invertebrates and most ectothermic vertebrates, where female-biased SSD is driven by strong fecundity selection in terms of increased investment in offspring production associated with larger female size (Abouheif and Fairbairn 1997; Blanckenhorn et al. 2007b; Stillwell et al. 2010). Fecundity and sexual selection for larger females or males is presumably held in

check by counteracting forces favoring small size in terms of adult and/or juvenile viability or survival, although empirical evidence for these selective processes is far scarcer and often difficult to come by (Blanckenhorn 2000). Additionally, the degree to which the sexes differ in size is also considerably affected by genetic, developmental and phylogenetic constraints (Badyaev 2002; Lindenfors et al. 2002; Ramos et al. 2005; Hu et al. 2010; Tammaru et al. 2010).

Although the above arguments intuitively explain variation in dimorphism among taxa, they are necessarily simplistic and incomplete because the crucial issue is the *relative* strength of sex-specific sexual, fecundity and viability selection in any given species (Price 1984; Arak 1988; Schluter et al. 1991; Andersson 1994; Blanckenhorn 2000). For example, strong sexual selection for large males also regularly occurs in species with smaller males (Andersson 1994; Fairbairn and Preziosi 1994; Fairbairn 1997; Blanckenhorn et al. 1999). In the ideal case, when all the relevant selection pressures are measured, the differential equilibrium model can generate quantitative predictions about the SSD expected of a given population or species (Arak 1988; Blanckenhorn 2000; Preziosi and Fairbairn 2000; Fairbairn et al. 2007). Therefore the model has to be tested in a micro-evolutionary context by comparing populations of a single species exhibiting variation in dimorphism (e.g. Storz et al. 2001; Schauble 2004; Teder and Tammaru 2005; McGarrity and Johnson 2009; Lyapkov et al. 2010; Yu et al. 2010). However, in most cases intra-specific variation in SSD is slight and quantitative but not qualitatively reversed. We know of only one study documenting albeit minor SSD reversals in some traits but not others in the house finch (Badyaev and Hill 2000). Here we investigate a unique example of strong

qualitative reversal in SSD among cross-continental populations of the dung fly *Sepsis punctum* (Fabricius, 1794; Diptera: Sepsidae).

Sepsidae are a family of flies with approximately 320 described species across 36 known genera. Like most insects, sepsid flies generally display female-biased size dimorphism, although examination of museum specimens indicates that in some species SSD is male-biased (Blanckenhorn et al. 2007b). *Sepsis punctum* in particular has a widespread distribution ranging from North America to Europe, North Africa and parts of Asia. It is a generalist that can be found on various types of decaying organic matter, although vertebrate excrements, and cow dung in particular, are its most common breeding substrate (Pont and Meier 2002). Schulz (1999; unpublished doctoral dissertation) first noticed that SSD might be reversed between European and Northern American *Sepsis punctum.* This situation presents the ideal opportunity to test the differential equilibrium model of SSD across replicate cross-continental *Sepsis punctum* populations that vary in both the direction and magnitude of SSD. Using laboratory common garden experiments, we first ascertain whether SSD is indeed male-biased in European and female-biased in American populations. Using standardized quantitative measures of selection (Lande and Arnold 1983; Arnold and Wade 1984a,b), we next estimate (i) adult viability selection on body size in terms of intrinsic (physiological) longevity, (ii) fecundity selection on female body size in terms of clutch and egg size, and (iii) sexual and fecundity selection on male body size in terms of male mating success and the number of eggs of his mate (assortative mating). We estimate sexual selection in population cages at three operational sex ratios (OSR), as a function of which competition for mates and consequently the intensity of sexual selection is expected to increase

(Bonduriansky 2001). According to the equilibrium model of SSD, we expect that in the European populations of *S. punctum* the intensity of sexual selection on male size should be greater than the intensity of fecundity selection on female size, whereas this should be reversed in North America; in other words, continental differences in sexual selection on male size should be large compared to continental differences in fecundity selection on female size and in viability selection on male and female size, which should be small or non-existent.

METHODS

Population sampling and fly culture maintenance

We sampled four European *S. punctum* populations from Nyköping, Sweden (SE: 58.67°N, 16.94°E), Berlin, Germany (DE: 52.45°N, 13.28°E), Vienna, Austria (A: 48.20°N, 16.36°E) and Zürich, Switzerland (CH: 47.40°N, 8.55°E), and three North American populations from Davis, California (CA: 38.54°N, -121.75°W), Athens, Georgia (GA: 33.96°N, -83.38°E) and Manhattan, New York (NY: 40.78°N, -73.96°E). Wild caught females were brought to the laboratory and used to establish stock cultures of multiple (10 to 20) replicate lines per population that were housed in separate plastic containers and regularly supplied with fresh cow dung, sugar and water *ad libitum*.

Common garden experiments

We conducted laboratory common garden experiments to ascertain patterns of SSD among the European and North American populations. We allowed mated females, housed in replicate group containers per population, to oviposit in pots of fresh cow dung for two to three hours. We then reared the offspring in groups in abundant cow

149 dung in a climate chamber at standardized 24^{o}C, 60% humidity and 14 h light cycle,
150 measured the development time and head width of emergent flies as a standard
151 index of body size. This method of using laboratory lines instead of wild caught
152 females removes confounding environmental variation influencing phenotypic body
153 size, establishing that the body size differentiation is indeed heritable.
154
155 **Testing the differential equilibrium model**
156 (i) Adult viability (i.e. intrinsic longevity) selection:
157 Viability selection on males and females is affected by multiple extrinsic factors such
158 as parasitism, predation, thermoregulation, food availability, etc. as well as by
159 intrinsic physiological and genetic factors (reflecting ageing). Estimation of juvenile or
160 adult mortality as a function of body size in the wild in small mobile insects is
161 essentially impossible. Instead we tested whether there are size- and sex-dependent
162 differences in intrinsic adult longevity between European and North American
163 populations as a function of body size under laboratory conditions in population
164 cages (cf. Blanckenhorn et al. 1999). We provided stock cultures with varying
165 amounts of dung to generate a range of phenotypic body sizes, and reared the
166 offspring under the standard conditions mentioned earlier. The emerging flies were
167 individually sexed under a microscope within 12 hours of eclosion and set up under
168 two different 'housing' treatments (Teuschl et al. 2010): males only and females only
169 (i.e. two treatments per population; five replicate containers per treatment; approx.
170 18-20 individual flies per container). Each container was provided with fresh dung,
171 sugar and water *ad libitum.* We monitored all 70 containers and more than 1300
172 individuals daily for adult mortality. Dead flies were removed every day, scored for
173 adult lifespan and measured for body size (head width).

174

175 (ii) Fecundity selection

176 To estimate fecundity selection, we randomly selected 30 – 60 once mated females
177 of various body sizes from the stock lines, set them up individually in glass vials,
178 provided them with fresh dung and counted their first (and sometimes additionally
179 their second) clutch sizes, which is good proxy for life-time fecundity in the study
180 species (Puniamoorthy unpublished data). Since investment in offspring production
181 can also be affected by the amount of resources invested in each egg, we
182 additionally measured the average egg volume of 5 eggs in each clutch for each
183 female in all seven populations. Every female was frozen afterwards and measured
184 for body size (head width).

185

186 (iii) Sexual selection: Male mating success

187 For each population, we supplied stock lines with two pots of fresh dung each. To
188 generate individuals of varying sizes, one dish was removed after two hours (no
189 larval competition) whilst the other was left overnight (competition). These dung
190 dishes were subsequently placed into larger plastic containers and housed in climate
191 chambers at 24 ^{o}C. Emerging flies were sexed within 24 hours of eclosion and
192 thereafter housed separately in single-sex group containers with dung, sugar and
193 water. We waited three to four days to ensure sexual maturity and then conducted
194 mating trials with randomly assembled virgin flies in population cages at three
195 operational sex ratios (OSR): 5 males plus 5 females (OSR = 1), 10 males plus 5
196 females (OSR = 2), and 20 males plus 5 females (OSR = 4). There were 4 – 5
197 replicates per OSR per population. Females always entered the population container
198 first, which was equipped with water and sugar and some fresh dung; the males

were added later. We tracked which male copulated with which female by isolating the mating pairs from the singletons. Each group trial lasted for a maximum of two hours after which all individuals (both mated and unmated) were measured for body size. From these data male sexual and fecundity selection differentials could be calculated (Supplementary file 1: Raw data).

In this study, since we were only interested in instantaneous pairing success, we did not allow for multiple mating. Early field observations of sepsid flies note that although male densities at a dung pat can rise up to 500 individuals in the first few minutes of the dung dropping, this number decreases drastically within the first 30 minutes (Hammer 1941). In fact, Parker (1972a, b) additionally showed that in *S. cynipsea,* the highest female arrival, oviposition and capture rates occur within ten minutes of the dropping and declines sharply after that. Copulation in *S. punctum* usually lasts approximately 20-30 minutes (Puniamoorthy, pers. obs.), during which time males are not available for re-mating. Hence, given that dung pats in nature become unattractive as oviposition sites quickly, multiple mating at the same dropping is relatively unlikely, so we believe our experimental setup simulates nature rather well.

Statistical Analysis

We used standardized regression methods to generate univariate linear selection differentials to assess the intensity of adult viability, female fecundity and male sexual and fecundity selection on (adult) body size (Lande and Arnold 1983; Arnold and Wade 1984a,b). In general, for each population and replicate container we produced standardized *z*-scores for body size (head width) by subtracting the

sample mean from each value and dividing the difference by the standard deviation: $z_i = (x_i - \bar{x})/SD_x$. Relative fitness was calculated as the absolute fitness component (i.e. adult longevity, female clutch and egg size, and male pairing success (1 or 0) or the body size of his female partner) divided by the population or container mean fitness (Arnold and Wade 1984b). We used models of relative fitness on z-scored body size $w = c + \beta_1 z$ to estimate univariate linear selection differentials.

To estimate viability selection, we regressed adult longevity on standardized body size, separately for the sexes and the replicate containers within populations. This yielded one viability selection estimate per replicate container. All 5 estimates per population were then averaged, yielding a corresponding confidence interval.

For female fecundity selection, we regressed relative clutch size or relative egg volume on standardized female body size. Selection coefficients of consecutive selection episodes are additive because fitness components are cumulative and hence multiplicative (Arnold and Wade 1984b). Thus, we can easily compute a female fecundity selection differential subsuming clutch and egg size. This yielded one fecundity selection differential per population with its appropriate standard error (or confidence interval) derived from regression.

A male's reproductive success is affected by both his mating success and the fecundity of his mate, which in turn depends on her body size (as above). We estimated sexual selection differentials based on mating success (males that copulated vs. those that did not) separately for each replicate container. Additionally, we regressed relative female body size (being proportional to her fecundity) on

standardized male body size. Adding (i.e. subsuming) both yielded the male fecundity selection differentials, one estimate per replicate container for all populations and OSRs, which were then averaged, yielding a corresponding confidence interval (see e.g. Blanckenhorn et al. 1999 for further details on these methods).

The above procedure describes calculation of the selection differential estimates. Significance testing, for all fitness components, was performed using the full models including continent, population nested within continent, replicate nested within population within continent (not applicable for female fecundity selection), and OSR (sexual selection only) as fixed or random factors and body size as a continuous covariate, including all relevant interaction terms. Variation in selection in all cases is established by significant factor by body size interactions. All analyses were done using the software SPSS version 10.0 (Norušis 2000).

RESULTS

Common garden experiments

SSD is clearly reversed comparing the two continents, with populations displaying male-biased SSD in Europe and female-biased SSD in North America (Figure 1; continent by sex interaction: $F_{1,5} = 27.88$, $P = 0.003$). Further, European flies are on average larger than North American flies and take longer to develop (Table 1; Body size: $F_{1,5} = 12.77$, $P = 0.016$; Development time: $F_{1,5} = 5.46$, $P = 0.067$; continent by sex interaction: $F_{1,5} = 10.22$, $P = 0.023$).

Testing the differential equilibrium model

(i) Adult viability (i.e. intrinsic longevity) selection:

Adult viability was overall slightly positively related with body size ($F_{1,1228}$ = 3.98, P = 0.046), thus implying no counterselection against large body size (contrary to expectation: cf. Blanckenhorn 2000). This effect could largely be attributed to the Austrian males and the New York population (both sexes); all other populations showed no effect whatsoever of body size on adult longevity (Table 2; mean level and range indicated in Figure 2). Standardized adult viability selection coefficients for males range between -0.048 ± 0.105 (95% CI) for the Swedish population and +0.157 ± 0.493 for the Austrian population; for females the range is from -0.010 ± 0.102 (95% CI) for the Georgian population and +0.079 ± 0.246 for the Austrian population (Table 2). There were strong systematic differences between the sexes in longevity (females living longer on average; $F_{1,1228}$ = 16.86, P < 0.001), some unsystematic variation among populations ($F_{5,28}$ = 2.55, P = 0.050), but no significant difference between the continents ($F_{1,28}$ = 0.04, P = 0.847; corresponding sex by factor interactions also n.s.). Viability selection for body size consequently was largely nil and did not vary systematically between the continents, the sexes, or the populations (all corresponding factor by body size interactions P > 0.1, except the three-way sex by population by body size interaction: $F_{5,1187}$ = 3.33, P = 0.005).

(ii) Fecundity selection

Larger females lay larger clutches in all populations (overall strong main effect of body size: $F_{1,317}$ = 610.58, P < 0.0001; Table 2). Standardized female fecundity selection coefficients based on clutch size range between 0.169 ± 0.057 (95% CI) for the California population and 0.343 ± 0.047 for the New York population (mean and range indicated in Figure 2; Table 2). Clutch size varied among populations within

299 continents ($F_{5,317}$ = 15.63, P = 0.001), but not between continents ($F_{1,5}$ = 0.63, P =
300 0.427). Crucially, fecundity selection differentials on body size (based on clutch size)
301 did not vary among populations within continents (population by body size
302 interaction: $F_{5,317}$ = 1.35, P = 0.244) or among continents (continent by body size
303 interaction: $F_{1,317}$ = 1.17, P = 0.280).
304
305 Overall, larger females also laid larger eggs (main effect of body size: $F_{1,175}$ = 15.85,
306 P < 0.001; Table 2), but the relationship with body size was much weaker.
307 Corresponding standardized female fecundity selection coefficients based on (cube-
308 root-transformed) egg volume range between 0.002 ± 0.010 (95% CI) for the
309 Swedish population and 0.020 ± 0.015 for the New York population. We had egg
310 volume data for about half of the clutches treated above, which varied
311 unsystematically among populations within continents ($F_{5,175}$ = 6.08, P < 0.001), but
312 not among continents ($F_{1,5}$ = 0.96, P = 0.443). However, when tested against the
313 global error, eggs were significantly smaller in North America than in Europe after
314 controlling for body size ($F_{1,175}$ = 6.01, P = 0.015). Nevertheless, fecundity selection
315 on body size based on egg volume did not vary among populations within continents
316 (population by body size interaction: $F_{5,175}$ = 0.49, P = 0.781) or among continents
317 (continent by body size interaction: $F_{1,175}$ = 2.10, P = 0.148).
318
319 (iii) Sexual selection:
320 In the European populations, 42 out of the 48 replicate sexual selection differentials
321 based on pairing success were positive, indicating strong sexual selection for larger
322 male body size. Further, sexual selection for large males intensified with increasing
323 OSR and with body size, supporting Rensch's rule (Figure 2). Sexual selection

differentials for the American populations were also generally positive (27 out of 36) albeit lower, but there was no clear pattern of increased selection with OSR (Figure 2; Table 2). The full (logistic) general linear model consequently indicated overall strong positive effects of body size (head width) on pairing success ($F_{1,930}$ = 22.23, P < 0.001), a significant interaction of continent and OSR ($F_{2,22}$ = 3.34, P = 0.044), and, most importantly, a significant OSR-by-continent-by-body size interaction ($F_{2,930}$ = 3.87, P = 0.021). The latter demonstrates variation in sexual selection on body size among the continents and the three OSR treatments.

Selection differentials reflecting assortative mating by size given pairing and hence the fecundity of the female partner were weak in comparison and did not vary significantly, ranging from -0.018 to 0.123; nevertheless, on average these added to the sexual selection differentials based on pairing success, making the combined male fecundity selection differentials even more positive across all populations and OSRs (73 out of 84) (Table 2).

DISCUSSION

We have shown here that a unique reversal in sexual size dimorphism between European and Northern American populations of the black scavenger fly *Sepsis punctum* is associated with, and presumably mediated by, substantial differences in the strength of positive sexual selection on males. As a result, European flies are larger than North American flies and SSD is male-biased and stronger, in agreement with Rensch's rule (Fairbairn 1997; Blanckenhorn et al. 2007b; Fairbairn et al. 2007). European females are also larger than North American females despite no differences in fecundity selection on female size, but this can be expected due to a

349 genetic correlation in body size between the sexes alone (Fairbairn 1997). In
350 European (but not North American) populations, sexual selection also increased with
351 the degree of male-male competition for females (i.e. the operational sex ratio:
352 OSR), as expected by sexual selection theory (Bonduriansky 2001). This outcome
353 confirms the differential equilibrium model of the evolution of SSD (Andersson 1994;
354 Preziosi and Fairbairn 2000; Blanckenhorn 2000).
355
356 We emphasize that while we were able to show an association between sexual
357 selection intensity and SSD (and probably mating system) evolution in accordance
358 with the differential equilibrium model, such evidence must remain correlational as
359 we cannot reconstruct the causality of evolutionary events. This is because
360 evolutionary shifts in mating behaviors and the mating system are expected to be
361 rapid and intimately associated with changes in sexual selection intensity, ultimately
362 affecting the evolution of body size and SSD (Ding and Blanckenhorn 2002).
363
364 We also emphasize that although we considered three major fitness components
365 (viability, fecundity, and sexual selection), comprehensive treatment of all relevant
366 aspects of selection affecting SSD evolution, let alone in the field, is virtually
367 impossible in any single species (Blanckenhorn 2000). In particular, we did not
368 assess juvenile viability selection on body size, which in animals with complex life
369 cycles such as insects is unattainable because larval and adult body size traits
370 cannot easily be compared and individuals that die before adulthood cannot be
371 measured (Blanckenhorn et al. 1999). One of the main mechanisms selecting
372 against large body size occurs because individuals often grow for longer time to
373 become larger, which increases cumulative mortality (Blanckenhorn 2000, 2007;

374 Blanckenhorn et al. 2007a). And indeed, European *S. punctum* have longer
375 development times than North American ones and the sex difference in development
376 time differs between continents (Table 1). However, because the differences in
377 absolute time are small (Table 1), it is doubtful that juvenile viability selection against
378 long development fully compensates the much stronger sexual selection for large
379 male size in European flies (cf. Blanckenhorn 2007). Furthermore, assessment of
380 intrinsic (i.e. physiological) adult viability in the laboratory, as done here, does not
381 necessarily reflect extrinsic adult viability in the field. Moreover, assessing female
382 fecundity selection in the laboratory is a limited approximation of reproductive output
383 in the field (Clutton-Brock 1988). Nevertheless, given no relationship of intrinsic
384 longevity (lifespan) with body size here, we have confidence in our estimates.
385
386 Recent comparative studies have highlighted the rapid divergence in sexual
387 dimorphisms and mating behavior in sepsid flies (Puniamoorthy et al. 2008;
388 Puniamoorthy et al. 2009; Tan et al. 2010). There have also been very early reports
389 of interesting courtship behavior in sepsid flies (Hammer 1941; Hafez 1948; Parker
390 1972a, b; Mangan 1976). In *S. punctum*, the cross-continental differences in SSD
391 documented here are accompanied by stark differences in the mating system (not
392 treated in detail here; Schulz 1999, unpublished doctoral dissertation). North
393 American populations display pre-copulatory courtship behavior in form of vigorous
394 shaking of the male abdomen when approaching the female, a behavior that is
395 absent in the European populations (Puniamoorthy et al., unpublished data). In
396 contrast, European males show no distinct pre-copulatory courtship but instead
397 scramble and/or contest competition among males, as evident by frequent male-
398 male mountings and common ‘take-overs’ where a male displaces another mounted

male (Parker 1972b; Zerbe 1993). In fact, our ongoing studies indicate that European females also re-mate more readily, whereas North American females re-mate very rarely (Puniamoorthy et al., unpublished data; cf. Teuschl and Blanckenhorn 2007). More detailed, in-depth behavioral studies of the systematic mating system differences between the continents should further help explain the reversal to male-biased SSD in Europe. Although the genetic distance between North American and European *S. punctum* is almost 3% (based on the DNA barcoding gene: R. Meier et al. unpublished data), European and North American flies readily hybridize and produce viable offspring (Schulz 1999; Puniamoorthy et al., unpublished data).

An increasing number of studies have documented considerable intra-specific variation in SSD, usually in response to environmental, latitudinal or even altitudinal clines (e.g. Badyaev and Hill 2000; Teder and Tammaru 2005; Fox and Czesak 2006; Stillwell and Fox 2007; Liu et al. 2010; Hu et al. 2011). Most of these studies treated (quantitative) variation merely in the magnitude of SSD. Our study is a unique exception in that we phenomenologically tested the differential equilibrium model of the evolution of SSD in a species showing strong qualitative variation in dimorphism. We could confirm the model by showing that sexual selection on male body size in *S. punctum* is consistently stronger in European than in North American populations, while fecundity selection acting on female body size and adult viability selection are weaker and not different between the continents. Unpublished molecular data by R. Meier and colleagues in Singapore (cf. Su et al. 2008) suggest that the SSD and mating system of North American *S. punctum* is the ancestral state as, like many invertebrates, most sepsid species display female-biased SSD. The

male-biased SSD in European *S. punctum* populations is therefore presumably secondarily evolved due to sexual selection in association with a change in the mating system, as predicted by theory (Andersson 1994; Fairbairn 1997; Bonduriansky 2001; Ding and Blanckenhorn 2002).

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643

644 **FIGURE LEGENDS**

645 Figure 1: Sexual body size dimorphism in 7 cross-continental populations of the
646 dung fly *Sepsis punctum* (Sample size: n_{europe} = 498, $n_{namerica}$= 618).

647

648 Figure 2: Mean fecundity (sexual) selection intensity on male body size in 7 cross-
649 continental populations of the black scavenger fly *Sepsis punctum* at three
650 operational sex ratios (OSR). White, grey and black boxes show selection intensity
651 increases with OSR (i.e. male competition). The (equal) levels of fecundity selection
652 on female body size (light grey bars; confidence limits) and of adult viability selection
653 (dark grey bars; confidence limits) on female and male body size do not differ
654 significantly between the continents.

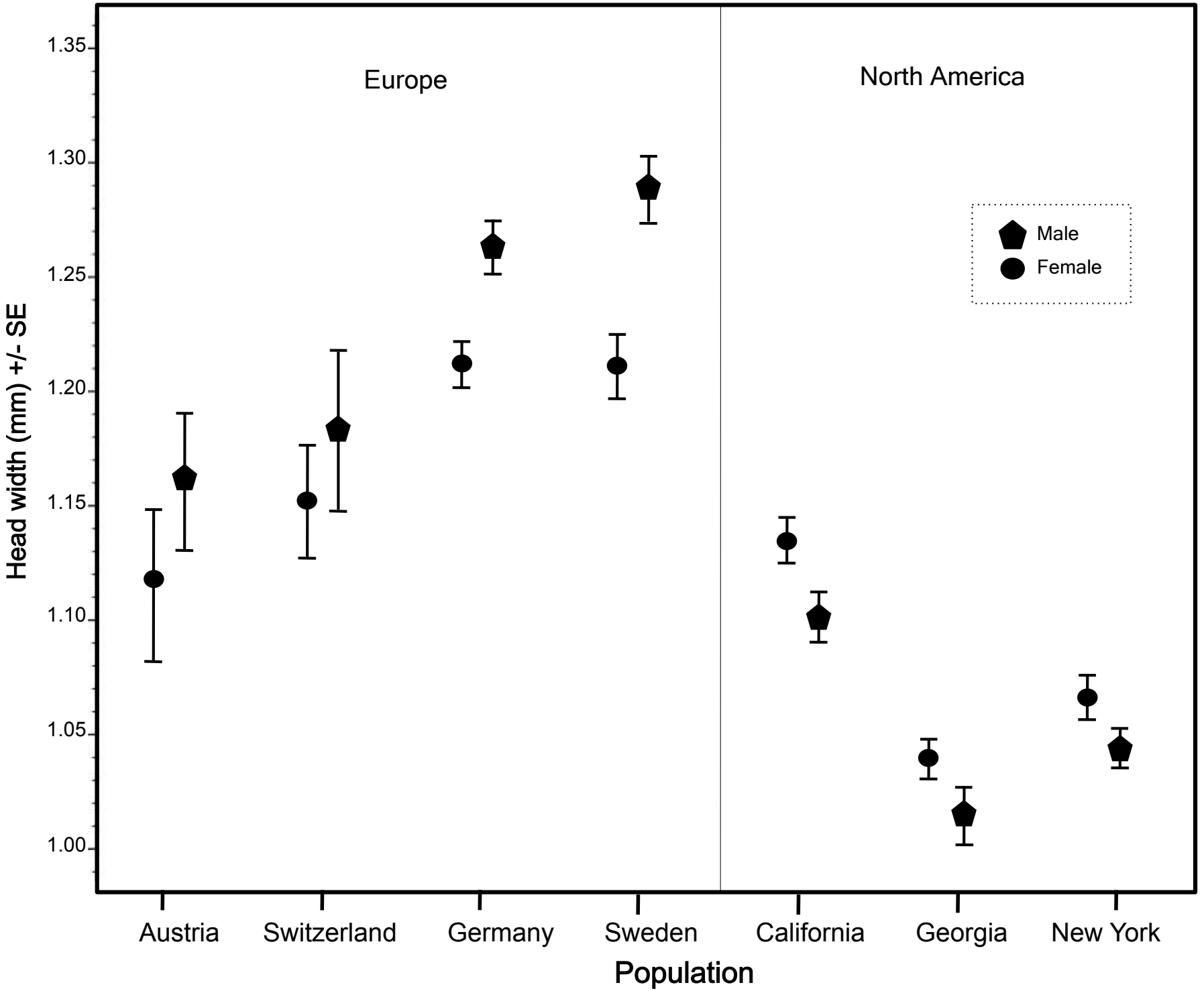
655

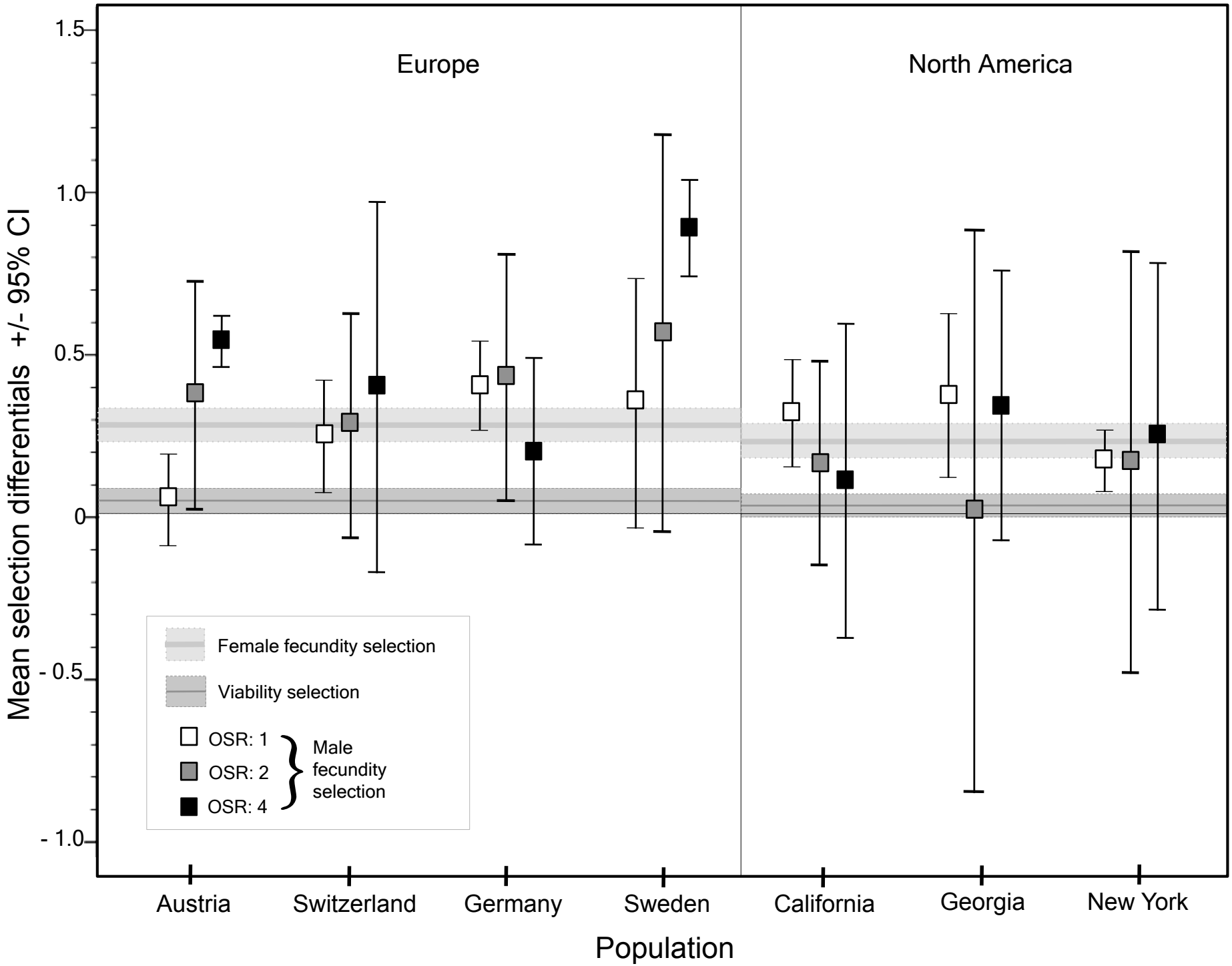
656 **TABLE LEGENDS**

657 Table 1: Population mean (± SE) for body size, development time, adult longevity,
658 female clutch size, egg volume and male pairing success (under different OSRs)
659 (Sample size, n).

660

661 Table 2: Univariate selection differentials (mean ± 95% CI) for adult viability selection
662 ($ß_{VS}$), female fecundity selection ($ß_{FS}$), male sexual selection ($ß_{SexS}$) and male
663 fecundity selection ($ß_{mFS}$).


Europe
North America
Male
Female
Head width (mm) +/- SE
1.35
1.30
1.25
1.20
1.15
1.10
1.05
1.00
Austria
Switzerland
Germany
Sweden
California
Georgia
New York
Population


Europe
North America
1.5
1.0
0.5
0
- 0.5
- 1.0
Mean selection differentials +/- 95% CI
Female fecundity selection
Viability selection
OSR: 1
OSR: 2
OSR: 4
Male fecundity selection
Austria
Switzerland
Germany
Sweden
California
Georgia
New York
Population

			Common garden				***Adult viability***				***Female fecundity***					***Male mating success***				
	Population	Sex	Head width (mm)	Development time (days)	n	"Housing" treatment	Head width (mm)	Lifespan (days)	n	Head width (mm)	First clutch	n	Egg volume	n	OSR	Head width (mm) Paired	n	Unpaired	n
Europe	Austria	Male	1.16 ± 0.07	14.25 ± 0.65	28	Male only	1.08 ± 0.07	69.16 ± 41.82	91						1	1.09 ± 0.16	22	1.09 ± 0.18	18
		Female	1.12 ± 0.10	13.54 ± 0.95	23	Female only	1.06 ± 0.05	77.24 ± 35.19	93	1.02 ± 0.13	81.03 ± 2.54	33	0.25 ± 0.01	33	2	1.02 ± 0.17	19	0.93 ± 0.15	22
															4	1.04 ± 0.19	22	0.92 ± 0.17	58
	Germany	Male	1.26 ± 0.04	14.45 ± 0.55	80	Male only	1.05 ± 0.13	48.23 ± 35.31	100						1	1.08 ± 0.54	20	1.04 ± 0.07	20
		Female	1.21 ± 0.03	13.54 ± 0.54	100	Female only	0.98 ± 0.13	62.15 ± 30.96	99	1.09 ± 0.11	59.61 ± 23.27	56	0.24 ± 0.01	19	2	1.09 ± 0.05	20	1.04 ± 0.06	20
															4	1.07 ± 0.06	19	1.05 ± 0.07	61
	Switzerland	Male	1.18 ± 0.14	15.40 ± 0.46	63	Male only	0.94 ± 0.10	74.55 ± 42.37	93						1	1.18 ± 0.09	22	1.14 ± 0.07	18
		Female	1.15 ± 0.09	14.91 ± 0.86	105	Female only	0.97 ± 0.10	71.42 ± 40.73	85	0.98 ± 0.13	69.83 ± 25.00	57	0.24 ± 0.01	20	2	1.18 ± 0.08	20	1.15 ± 0.07	20
															4	1.18 ± 0.09	21	1.14 ± 0.07	60
	Sweden	Male	1.29 ± 0.06	14.6 ± 0.88	47	Male only	1.36 ± 0.13	51.97 ± 27.00	98						1	1.13 ± 0.18	21	1.02 ± 0.15	19
		Female	1.21 ± 0.05	14.27 ± 0.84	52	Female only	1.07 ± 0.10	65.42 ± 31.60	100	1.06 ± 0.14	89.80 ± 27.90	30	0.26 ± 0.01	29	2	1.16 ± 0.12	20	0.99 ± 0.15	20
															4	1.21 ± 0.10	20	1.00 ± 0.17	60
North America	California	Male	1.10 ± 0.03	13.93 ± 0.72	83	Male only	0.97 ± 0.04	68.70 ± 36.43	91						1	1.01 ± 0.08	21	0.99 ± 0.09	19
		Female	1.14 ± 0.03	13.72 ± 1.81	127	Female only	1.00 ± 0.05	59.66 ± 34.27	87	1.03 ± 0.10	68.40 ± 18.00	47	0.24 ± 0.01	34	2	1.01 ± 0.08	18	0.98 ± 0.09	22
															4	1.00 ± 0.08	16	1.00 ± 0.09	59
	Georgia	Male	1.02 ± 0.04	12.29 ± 0.86	66	Male only	0.84 ± 0.10	55.93 ± 33.41	98						1	0.90 ± 0.06	27	0.82 ± 0.09	23
		Female	1.05 ± 0.03	12.55 ± 1.00	67	Female only	0.87 ± 0.09	78.76 ± 34.66	101	0.94 ± 0.07	71.79 ± 14.52	46	0.24 ± 0.01	40	2	0.92 ± 0.07	15	0.92 ± 0.08	25
															4	0.96 ± 0.03	18	0.93 ± 0.07	58
	New York	Male	1.05 ± 0.03	14.34 ± 0.78	112	Male only	0.98 ± 0.04	51.30 ± 24.37	79						1	1.02 ± 0.03	19	1.00 ± 0.04	19
		Female	1.07 ± 0.03	14.69 ± 0.84	163	Female only	1.00 ± 0.05	60.22 ± 33.08	102	0.95 ± 0.13	64.42 ± 24.94	58	0.24 ± 0.01	16	2	0.99 ± 0.03	14	0.99 ± 0.04	28
															4	1.00 ± 0.04	13	0.99 ± 0.04	66

Table 1: Population mean (± SE) for body size, development time, adult longevity, female clutch size, egg volume and male pairing success (Sample size, n).

	Population	"Housing" treatment	Adult viability $ß_{VS}$	Female fecundity $ß_{FS}$	OSR	Male reproductive success $ß_{SexS}$	$ß_{mFS}$
Europe	Austria	Female only	0.079 ± 0.246	0.248 ± 0.127	1	0.013 ± 0.177	0.040 ± 0.177
		Male only	0.157 ± 0.493		2	0.324 ± 0.436	0.363 ± 0.436
					4	0.438 ± 0.095	0.532 ± 0.095
	Germany	Female only	0.020 ± 0.148	0.326 ± 0.053	1	0.311 ± 0.165	0.428 ± 0.165
		Male only	-0.030 ± 0.105		2	0.427 ± 0.475	0.418 ± 0.475
					4	0.208 ± 0.356	0.190 ± 0.356
	Switzerland	Female only	0.013 ± 0.223	0.291 ± 0.057	1	0.179 ± 0.215	0.302 ± 0.215
		Male only	0.009 ± 0.163		2	0.206 ± 0.422	0.219 ± 0.422
					4	0.388 ± 0.698	0.389 ± 0.698
	Sweden	Female only	0.026 ± 0.127	0.263 ± 0.063	1	0.306 ± 0.474	0.340 ± 0.474
		Male only	-0.047 ± 0.020		2	0.521 ± 0.756	0.557 ± 0.756
					4	0.876 ± 0.178	0.881 ± 0.178
North America	California	Female only	0.016 ± 0.165	0.169 ± 0.057	1	0.260 ± 0.198	0.310 ± 0.198
		Male only	-0.004 ± 0.157		2	0.163 ± 0.385	0.154 ± 0.385
					4	0.117 ± 0.598	0.099 ± 0.598
	Georgia	Female only	-0.010 ± 0.102	0.170 ± 0.033	1	0.329 ± 0.393	0.362 ± 0.393
		Male only	0.032 ± 0.181		2	0.015 ± 1.064	0.007 ± 1.064
					4	0.342 ± 0.511	0.330 ± 0.511
	New York	Female only	0.025 ± 0.131	0.343 ± 0.047	1	0.053 ± 0.120	0.163 ± 0.120
		Male only	0.068 ± 0.338		2	0.155 ± 0.799	0.157 ± 0.799
					4	0.229 ± 0.659	0.237 ± 0.659

Table 2: Univariate selection differentials (mean ± 95% CI) for adult viability selection ($ß_{VS}$), female fecundity selection ($ß_{FS}$), male sexual selection ($ß_{SexS}$) and male fecundity selection ($ß_{mFS}$)